Ecology and conservation of the Pale-headed Snake (*Hoplocephalus bitorquatus*, Elapidae)

Mark Fitzgerald[1]**, Brian Lazell**[2]**, Richard Shine**[1,*]

[1]School of Biological Sciences A08, University of Sydney, NSW 2006, Australia
[2]53 Curtin Street, Cabramatta, NSW 2166, Australia

*To whom correspondence should be addressed: rics@bio.usyd.edu.au

ABSTRACT

The Pale-headed Snake, *Hoplocephalus bitorquatus* (Jan 1859), is a slender-bodied, arboreal, venomous snake that is widely, but patchily, distributed through coastal and inland eastern Australia. We summarise existing knowledge on the conservation status and the ecology of this taxon, and provide original data based on fieldwork at a study site on the Namoi River (a river red gum - coolabah woodland). Four radio-tracked snakes spent long periods hidden within tree hollows, usually in Coolabah Trees. The telemetered snakes moved infrequently, with one gravid female remaining within the same tree for 61 days. Overall, strong similarities are evident between the Pale-headed Snake and two congeneric species that have attracted more detailed previous research. Those similarities, and the range of threatening processes affecting inland riparian ecosystems, suggest that the Pale-headed Snake may be of significant conservation concern and thus, warrant more intensive study.

Key words: Ambush predator, arboreality, radiotelemetry, reptile

Introduction

Although there are more species of reptiles than of mammals in Australia, the ecology and conservation status of the former group has attracted far less scientific attention than has the latter (Cogger *et al.* 1993). This bias is not restricted to Australia, with the conservation status of reptiles very poorly understood worldwide (Gibbons *et al.* 2000; Cogger 2001). Accordingly, current conservation priorities for reptiles tend to be based largely on guesswork and subjective evaluation, with few robust data sets on population demography or threatening processes. One likely result of that ignorance is that we have little real idea of which species are most at risk.

In an attempt to identify snake taxa of conservation concern, Reed and Shine (2002) analysed a large database on life-history characteristics of Australian species (derived primarily from dissection of preserved museum specimens). The analysis revealed several correlates of conservation status (as ranked by Cogger *et al.* 1993), and identified a series of other species (not currently identified as "at risk") exhibiting traits that apparently predispose species towards endangerment. Clearly, additional ecological information on these species should be a high priority for conservation-relevant research (Reed and Shine 2002).

The present paper focuses on one of the snake species identified as potentially "at risk" from Reed and Shine's analysis. It is the Pale-headed Snake, *Hoplocephalus bitorquatus*, a slender-bodied arboreal proteroglyphous (elapid) species with a broad but patchy distribution in eastern Australia from near Wyong on the central coast of New South Wales to Mt Surprise and Innot Hot Springs in far north Queensland. The Pale-headed Snake is absent or unrecorded over a wide area of the dry tropics in Queensland (Longmore 1986) and the species' range appears to be disjunct, with the far north Queensland population widely isolated from more southern populations (Wilson 2005). Thus, although the species is found over an immense area, it is uncommon and patchily distributed (Ehmann 1992). The Pale-headed Snake *H. bitorquatus* is listed on Schedule 2 of the *Threatened Species Conservation Act* 1995 as 'Vulnerable' in New South Wales, based on an assessment that "Population suspected to be reduced; distribution severely reduced; threatening processes moderate; ecological specialist" (Lunney *et al.* 2000). Its two congeners (*H. bungaroides* and *H. stephensii*) both have long been listed as of conservation concern (Jenkins 1985), further suggesting that *H. bitorquatus* populations also may be at risk.

A review of existing information on the biology of *H. bitorquatus*

Geographic range in New South Wales

In New South Wales the species is recorded from the following bioregions: Darling Riverine Plains, Brigalow Belt South, Nandewar, New England Tableland, NSW North Coast and Sydney Basin.

Arboreality

The Pale-headed Snake is a slender-bodied nocturnal tree-climbing elapid (Figure 1) that is seldom encountered by humans. Pale-headed Snakes are unusual among Australian snakes in being highly adapted for life in the trees (Shine 1983). All three

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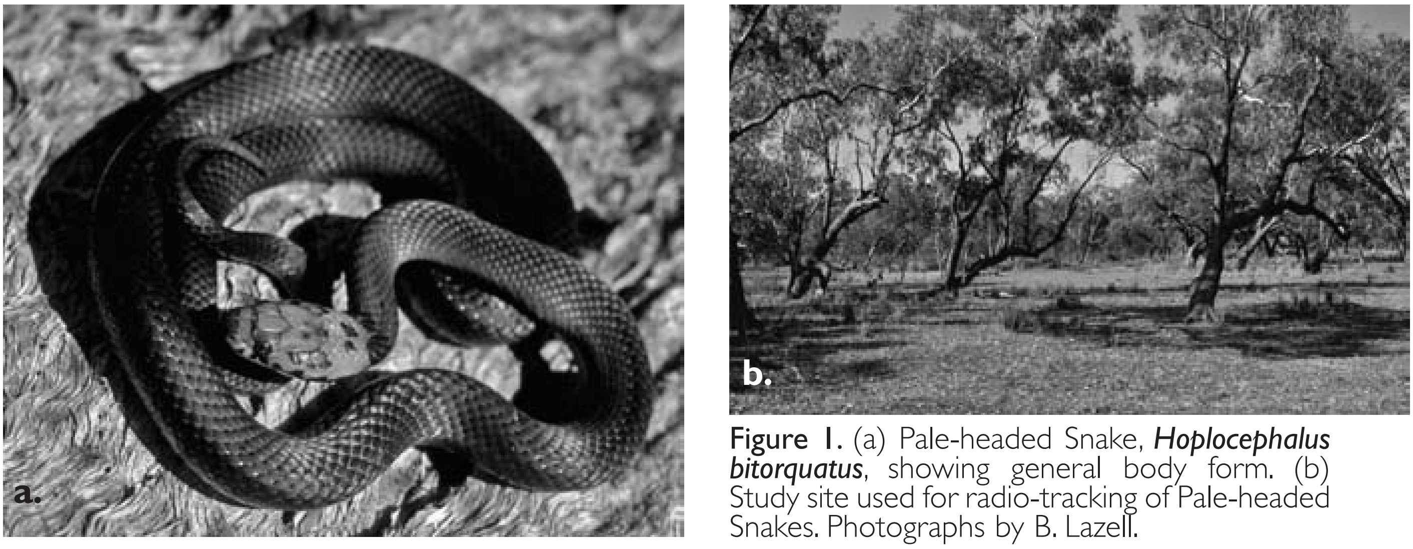

Figure 1. (a) Pale-headed Snake, ***Hoplocephalus bitorquatus***, showing general body form. (b) Study site used for radio-tracking of Pale-headed Snakes. Photographs by B. Lazell.

Hoplocephalus species possess a sharp-edged keel along either side of the belly. The keels, present in many other arboreal snake species, are used to grip small irregularities on the tree surface and to climb smooth bark (e.g. upper branches of River Red Gum *Eucalyptus camaldulensis*). This keel enables Pale-headed Snakes to exploit trees (particularly, hollows and the space between the decorticating bark and bole of standing trees) as foraging and shelter sites.

Reproduction

Much of what is known of the biology of Pale-headed Snakes derives from dissection and examination of museum specimens (Shine 1983). This work revealed that in NSW male Pale-headed Snakes (average size 47.5 cm SVL [= snout-vent length]) are smaller than females (average SVL = 55.6 cm). In Shine's sample, snakes from NSW were slightly larger than Queensland specimens.

All *Hoplocephalus* species are viviparous. Sexual maturity (determined by examination of male testes and efferent ducts, and female ovarian follicles) occurs at about 37.6 cm (male) and 40.2 cm (female) SVL (Shine 1983). In the same study, litter size averaged 4.7 young and the smallest individual was ~18 cm SVL. Reproductive frequency is low; few females in the sample were reproductive, suggesting that reproduction takes place less than annually (as appears to be the case also with both congeners, *H. bungaroides* and *H. stephensii*: Webb and Shine 1998a; Fitzgerald *et al*. 2004). In keeping with these data, captive Pale-headed Snakes produced small litters (range 3 to 6) of relatively large offspring (20 to 23 cm SVL: Lazell 2000). Female investment in reproduction was high, with RCM (= maternal mass divided by maternal post-partum mass) ranging from 0.60 to 0.75 (Lazell 2000, 2007).

Habitat

Pale-headed Snakes have been recorded from a range of forest and woodland habitats. Most published descriptions of habitat are general in nature, e.g. "From rainforests to the drier sclerophyll forests on the western slopes" (Swan 1990); "Dry sclerophyll forests and woodlands (occasionally rainforests or wet sclerophyll forests)" (Wilson and Knowles 1988). Recent records of this species west of the Great Dividing Range in NSW include sites dominated by Narrow-leaved Ironbark (*E. crebra*) forest with cypress pine (*Callitris* spp., M. Fitzgerald pers. obs.); Black Box (*E. largiflorens*) and Silver-leaf Ironbark (*E. melanophloia*) woodland and Coolabah (*E. coolabah*) (Michael Pennay, NPWS, pers. comm.). Records from near-coastal locations include Broad-leaved Ironbark (*E. fibrosa*), Spotted Gum (*Corymbia maculata*), Forest Red Gum (*E. tereticornis*) and Grey Gum (*E. propinqua*) forests (M. Fitzgerald pers. obs.). Habitat near the south-eastern limit of the range includes rainforest. Because Pale-headed Snakes eat frogs (see below), populations may tend to be associated with watercourses, billabongs and other flood-prone areas.

Diet

Pale-headed Snakes in museum collections contained one scincid lizard, three gecko species, five frog species and one small mammal species (House Mouse, *Mus domesticus*). Twenty of the twenty-six food items (~77%) in museum specimens were frogs (Shine 1983). Bats also may be eaten (Ehmann 1992). Additional prey records regurgitated by captured snakes include the gecko *Gehyra dubia* and the tree frog *Litoria peronii* (Lazell 2007). The frequent occurrence of subcutaneously encysted tapeworm larvae (sparganids) in Pale-headed Snakes (Lazell 2007, and see below) supports the conclusion that frogs are a major component of the diet.

Methods for Field Study

Radio-tracking

Field research was focussed at a riparian site beside the Namoi River between Pilliga and Burren Junction (elevation 160 m asl). Large River Red Gums (*E. camaldulensis*) were common, with extensive mature Coolabah/Black Box (*E. coolabah, E. largiflorens*) woodland on riverbanks and adjacent river flats. Emu bushes (*Eremophila* sp.) and River Cooba (*Acacia* *stenophylla*) were present also. Little groundcover other than sparse grasses was present on the northern side of the river, with Lignum (*Muhlenbeckia florulenta*) on the lower southern side. Soil is heavy dark brown to dark grey cracking clay and the topography is near level. Sheep and cattle graze in all parts of the main study site. We do not provide an exact locality, so as not to facilitate illegal collecting.

Nocturnal foot-based searches of trees and the ground beneath trees with spotlights (Nov 2001 – March 2002) yielded 18 snakes under a range of climatic conditions. In December 2001, we surgically implanted miniature temperature-sensitive radiotransmitters (BD-2GT, Holohil, Canada) in four relatively large snakes (47, 57, 95 and 110 g; 55.0, 55.0, 58.5, and 64.5 cm). Transmitters were implanted in the lower peritoneal cavity following methods used for other *Hoplocephalus* species (Webb and Shine 1997a; Fitzgerald *et al*. 2002a). The two smaller snakes were equipped with 1.85 g transmitters, the larger two with 2.65 g transmitters. Transmitter antennae were fitted with a soft, flexible silastic catheter plugged distally with flowable 'Silastic' silicon (Dow Corning). Transmitters were calibrated in a water bath in 5°C increments between 5 and 40°C. Data on the relationship between temperature and signal interval (in milliseconds, obtained using a stopwatch over 10 pulse intervals) were later used to determine body temperatures of the telemetered snakes. All snakes recovered well from surgery and were released at their capture locations (10/12/2001). Each time a telemetered snake was radio-located, we recorded location, time, telemetry pulse interval, date, habitat, microhabitat, posture, % body exposed, % canopy cover, distance to nearest tree, height above ground, visibility of snake to observer (yes/no), and the distance and direction that the snake had moved from its previous location.

Structural and taxonomic characteristics of the trees upon which Pale-headed Snakes were seen (either at initial capture or during radiotelemetry) were measured and categorized. We recorded tree species, diameter at breast height (cm; measured with dbh tape), number of stems at breast height, height (m; using a Suunto clinometer), form (single tree, or multi-trunked clump as in some *E. camaldulensis*), and life form, (adapted from Gibbons and Lindenmayer's [1997] 9-stage key to the forms of hollow-bearing trees based on successional stages. As only live trees were used by snakes, categories are: 0 = live tree with no hollows; 1 = mature tree with canopy intact and hollows present; 2 = mature tree with dead branches in the canopy), % canopy cover (by comparing with figures in McDonald *et al*. 1990), bark roughness (divided into three categories: 1 = immature red gum, 2 = mature red gum or coolabah, 3 = extensive thick decorticating bark), presence and number of branch hollows (in three categories: 0 = no branch hollow; 1 = 1 branch hollow; 2 = >1 branch hollow), trunk hollow (in three categories: 0 = no trunk hollow; 1 = 1 trunk hollow; 2 = >1 trunk hollow), distance to nearest tree (m), distance to watercourse (m). Tree data are presented in Table 1.

Thermal monitoring

To quantify thermal conditions at the study site, we deployed six thermal data-loggers (Thermochron i buttons; Dallas Semiconductor, Dallas, USA; diameter 15 mm, height 6 mm) in three different situations. Because Pale-headed Snakes sheltered in tree hollows, we placed two data-loggers within cavities in live trees and two within cavities in dead trees. We placed the remaining two data-loggers in painted copper tubes (mimicking dorsal colouration of the snakes) on the ground in sun-exposed situations. The data-loggers recorded temperatures every two hours from 12–30 December 2001.

Results of Field Study

Morphology

Of 17 snakes captured at the study site, all were adults (8 males, 9 females). Body sizes were similar in the two sexes: males averaged 50.1 cm SVL (range 39-58.5 cm; SD = 7.46; n = 8), as did females (range 42-64.5 cm, SD = 6.93; n = 9). Body masses of the two sexes were similar also, with males averaging 46.4 g (range 17.5-110 g, SD = 29.06; n = 8) and females averaging 43.3 g (range 17-95 g, SD = 27.30; n = 9). Thus, neither mean body length nor mean body mass differed significantly between the sexes (ANOVA: SVL, $F_{1,15} = 0.05$, $P = 0.82$, and mass, $F_{1,15} = 0.001$, $P = 0.99$).

Approximately half the snakes at the study site exhibited overt bulges in the skin containing encysted tapeworm larvae, and one snake was infested with the exotic mite *Ophionyssus natricis* when captured (identified by D. Walter, University of Qld).

Habitat use

Despite searches extending >200 m from the river, no snake was located >160 m from the river. Twenty-one night's collecting effort at the study site between November 2001 and March 2002 resulted in the capture of 17 Pale-headed Snakes (plus, an additional gravid female was sighted in an inaccessible position). In addition to the four snakes radio-tracked, three others were later relocated on a total of six occasions. Three females were gravid when observed (November 17; January 9 and 19). This represents the largest single sample of the species reported in NSW and the first radio-tracking study for this species.

Snakes were captured over 11 nights between 2043 and 2255 h. Relative humidity at the time of capture varied from 30% to 61% (mean = 46.3%, SE = 3.8). Shaded air temperatures taken at each radio-tracking location varied from 20-30°C (mean = 23.76°C, SE = 0.65). When first seen, three snakes were moving on the ground and 15 were in trees. Two snakes were captured on the ground at the base of trees, so these trees were included in the "capture tree" sample. The trees in which snakes were originally captured were River Red Gums *E. camaldulensis* (7), Coolabah *E. coolabah* (7), Black Box *E. largiflorens* (1), and River Cooba *A. stenophylla* (1). Coolabah (9) and Black Box (5) were the tree species most frequently used by radio-tracked snakes, with River Red Gum (2), River Cooba (1) and unidentified eucalypts (2) also used.

Table 1. All trees (*n* = 35) recorded as being used by Pale-headed Snakes in the course of the field study. Life form categories are based on the classification by Gibbons and Lindenmayer (1997). *Stage = key to the forms of hollow-bearing tree based on successional stages (Gibbons and Lindenmayer 1997).

Tree species	Snake height above ground (m)	Diameter at breast height (cm)	Number of stems at breast height	Tree height (m)	Single or multi-trunk?	Stage*	% canopy cover	Bark roughness	Number of branch hollows	Number of trunk hollows	Distance to nearest tree (m)	Distance to nearest watercourse (m)
Eucalyptus camaldulensis	1.5	44.5	1	16	multi	0	25	2	0	0	0	25
Eucalyptus camaldulensis	3.5	135	1	32	single	2	20	2	1	1	12	30
Eucalyptus coolabah	1.5	185	4	14	single	1	30	3	1	2	3	25
Eucalyptus largiflorens	0	76.3	1	18.5	single	1	35	3	2	2	4	80
Eucalyptus coolabah	1.9	62.7	1	17.5	single	1	30	3	1	0	6	40
Eucalyptus coolabah	0	210.3	7	20	single	1	45	3	0	2	8.5	65
Eucalyptus camaldulensis	1.6	122	1	17.5	single	2	30	2	1	1	4.5	10
Eucalyptus coolabah	1.6	99.5	1	20.5	single	1	40	3	1	1	6	20
Eucalyptus coolabah	1.2	79.6	1	22.5	single	1	30	3	0	2	5.5	63
Acacia stenophylla	1.1	35	2	6	single	1	15	2	0	0	2.5	30
Eucalyptus coolabah	1.5	96.9	1	16	single	1	25	2	2	0	5	45
Eucalyptus camaldulensis	0.7	69.3	2	15	multi	0	25	1	0	0	1	30
Eucalyptus camaldulensis	3	200	1	20	single	1	25	1	2	1	1	10
Eucalyptus coolabah	0.8	53.4	2	9	multi	1	20	2	1	0	3	35
Eucalyptus camaldulensis	3	167.4	1	26	single	2	30	1	2	1	11	60
Eucalyptus camaldulensis	4	174.3	1	29	single	2	25	2	2	2	11	50
Eucalyptus camaldulensis	2.5	87	1	17	single	1	40	2	1	1	6	35
Eucalyptus camaldulensis	0.8	66.5	2	7	multi	1	35	2	2	2	5	65
***Eucalyptus* sp.**	0.1	53.9	2	9	single	1	25	2	0	1	9	45
Eucalyptus largiflorens	5	81.2	1	18	single	1	35	2	1	2	10	80
Eucalyptus largiflorens	5.5	126.4	2	17	single	1	35	2	2	1	10	90
Eucalyptus largiflorens	3.5	110.5	1	12	single	1	30	2	2	1	15	110
Eucalyptus coolabah	5	50.5	1	15	single	1	15	2	2	0	11	55
Eucalyptus coolabah	5	63.8	2	13	single	1	35	2	2	1	11	60
Eucalyptus coolabah	4	110	1	20	single	1	35	2	1	1	13	30
Eucalyptus largiflorens	6	72.9	1	16	single	1	35	2	2	1	11	35
Eucalyptus coolabah	4	88	1	9	single	1	20	2	2	1	5	30
Eucalyptus largiflorens	4	136	1	18	single	1	30	2	2	1	3.5	20
Eucalyptus coolabah	0.5	209.3	5	16	multi	2	35	2	2	1	3.5	30
***Eucalyptus* sp.**	4	69.6	2	15	single	1	35	2	2	1	10	130
Acacia stenophylla	2	14.4	1	3.5	single	1	10	2	0	0	1.5	25
Eucalyptus coolabah	n/a	94.3	2	14	multi	1	30	2	2	1	13	125
Eucalyptus coolabah	3.5	87.4	3	17	multi	1	25	2	2	1	4.5	160
Eucalyptus coolabah	3.5	115.7	2	15	multi	1	20	2	2	1	4.5	30
Eucalyptus coolabah	0.8	121.9	2	17	multi	1	30	2	2	0	10	40

Snakes in trees were either located on the trunk (*n* = 8) or in the lowest fork (7) and were characterised to be in ambush posture (2), climbing down (2), perched (6) or actively searching (5). Mean height above ground of snakes captured in trees was 1.68 m (SE = 0.29). On the first visit to the site (14 to 19 November 2001), we captured nine snakes over four nights. Frog activity levels were increased following rain on 16 November 2001, possibly influencing snake activity.

Sixteen trees where snakes were initially captured, and 19 trees used by radio-tracked snakes when we located them, were sampled. All trees used by snakes were live and ranged from 3.5 to 32 m in height (mean = 16.22 m, SE = 0.99). Diameter at breast height of trees ranged from 14.4 cm to 210.3 cm (mean = 102.1 cm, SE = 8.48). It is difficult to estimate the number of available hollows in trees (Mackowski 1987), especially because adult snakes are able to gain access to the interior hollows of trees through very small openings (~10 mm). Thus, we scored the abundance of hollows in trees used by snakes according to categories. Most (88.6%) trees used by snakes had either branch hollows or trunk hollows and 65.7% had both. The most frequent hollow score was >1 branch hollow, plus 1 trunk hollow (37.1% of trees). About half (18 of 35) of the trees used by snakes had at least three hollows.

In terms of both height and girth, River Red Gums were the largest trees used by snakes. Mean hollow scores were highest for Black Box, followed by Coolabah then River Red Gum. The smallest two trees used by snakes were River Cooba *A. stenophylla*. These shrub-like small trees do not appear to contain hollows, but decorticating bark develops in mature and senescing specimens (M. Fitzgerald pers. obs.) and was present in the two trees used by Pale-headed Snakes. When found on a River Cooba at night, snake #10 was foraging (moving slowly, tongue-flicking frequently and pausing). It seems likely that the snake was searching for prey on these trees. The discovery of a red-naped snake (*Furina diadema*) foraging at night in a similar mature River Cooba suggests that snakes search for skinks on such trees. Red-naped snakes exclusively feed upon scincid lizards (Shine 1981).

Pale-headed Snakes also are found under decorticating bark (Swan 1990; M. Fitzgerald pers. obs.). Two types of bark are present on the River Red Gums used by the snakes. Relatively fine seasonally shed bark appears on the upper branches and trunks of these trees and occasionally accumulates in stacked layers in branch forks. It is also seasonally present as adherent sheets, often curled inward at the edges, on the bole and branches of trees. Tree frogs (*Litoria caerulea, L. peronii, L. rubella*) observed in river red gums at the study site at night may shelter by day beneath decorticating bark.

Bark of the basal stocking of larger River Red Gums is much thicker and more plate-like, and may adhere for much longer. Decorticating bark was not common in Coolabah or Black Box but was present on both River Cooba used by snake #10. Snakes found active at night on four trees without hollows were most likely foraging in decorticating bark (see below).

Radio-tracking results

Snakes were mainly radio-tracked by day, during six separate visits to the site from December 2001 to April 2002. One snake disappeared soon after release (#6) possibly due to predation and removal: this transmitter was later found ~350 m inland from the snake's capture site). The other three snakes were tracked on visits of 2 to 5 days each for total periods of from 4 to 139 days. Fifty-four separate radio-tracking observations revealed the use of 15 trees.

On eight occasions when snakes were located at night, two of these animals were engaged in arboreal foraging (described below); in the other six cases the animals remained hidden within tree hollows. Snakes active on the surface of trees at night are readily seen, but telemetered snakes located in trees by day were entirely hidden within tree cavities. In 96.3% of radio-tracking observations, snakes were sequestered in tree hollows. Trunk hollows were used most (70.4%) with less frequent use of branch hollows (18.5%) and of a hollow tree root (7.4%). Most mature trees at the site had hollows (e.g. 55% of 100 randomly sampled trees), and many had numerous entrances to the main trunk hollow.

Pale-headed Snakes spend long periods of time sequestered in tree hollows. A telemetered gravid female snake (#8) was relocated in the same tree over 61 days. It is doubtful that she left the tree during this period. Male #3 was located in the same tree from 14 Dec 2001 to 10 Jan 2002. Determining the precise duration of tree hollow sequestration is rendered problematic by the intermittent timing of our radio-tracking, because the extent of snake movement between visits remains unknown.

Twenty of the snake displacement events that we observed were between shelter trees. The distances moved ranged from 10 to 135 m (mean = 53.27 m, SE = 9.14). The diel timing of movements is unknown, but initial capture times of snakes moving on the ground were 2056, 2145 and 2250 h. Snake #3 was located moving on the ground at 2205 on 13 Feb 2002 and was followed using a dimmed torch beam. In 45 minutes he travelled 42 m to ascend a tree previously used by him from 27 Dec 2001 to 10 Jan 2002. Additional data on snake movement and philopatry were derived from sightings of snakes earlier captured but not radio-tracked. One male snake (#1) was seen on the same tree on five occasions (14 Nov 2001 to 9 Jan 2002). Another male (#10) was found in an *A. stenophylla* on 10 Dec 2001, and in another tree of the same species 85 m away two nights later. A female (#13) found in a *E. camaldulensis* on 27 Dec 2001 was seen in the same tree on 9 Jan 2002.

Two telemetered snakes were found actively foraging at night on the surface of trees. Snake #4 was located foraging on the surface of his daytime shelter tree at 2000 h on 11 Feb 2002 and snake #3 was observed foraging on a tree on the same night at 2100 h. Snake #3 did not shelter in this tree and was next day located 100 m distant in a previously unused tree. Air temperatures were 24°C for both observations. Foraging behaviour for both snakes involved tongue-flicking at the tree surface and the exploration of small cavities on the tree surface, including placing the head and neck into cavities large enough to permit ingress. The duration of observations was ~20 min on each occasion. Body temperature for snake #4 while foraging was 31.2°C. Five snakes appeared to be foraging at the time of initial capture, searching tree surfaces slowly and tongue-flicking frequently. Ambush is also likely to be used to acquire prey. At initial capture two snakes were found in an ambush posture, stationary with the posterior body anchored beneath decorticating bark and the neck looped in a broad coil.

Limited data are available to clarify the size of areas used by snakes. A gravid female (#8) was extremely sedentary, moving only once (a distance of 20 m) in 61 days. That move was possibly in response to her shelter tree being attacked with an axe to open a native bee colony. Because radio-tracking took place on six separate visits from 11 December 2001 to 30 April 2002, activity areas are likely to be underestimates. Based on seven and eight moves respectively, activity areas for two adult male Pale-headed Snakes were estimated to be 2288 m^2 and 2156 m^2.

Both males returned to a previously used tree on one occasion and used five and eight trees respectively. Three snakes (2 female, 1 male) were captured inside the activity area occupied by one telemetered male (#3) and the dense concentration of animals (18 snakes in 15 ha) suggests that home ranges either are very small, or overlap substantially. This differs from the spatial ecology of the congeneric *H. stephensii*, in which radio-tracked individuals tended to avoid each other's presence (Fitzgerald *et al.* 2002b).

Thermal monitoring

Body temperatures of radio-tracked snakes ranged from 17.9 to 33.5°C (mean = 25.5°C; SE = 0.49; *n* = 42), while simultaneously-recorded shaded air temperatures ranged from 19 to 32.5°C (mean = 25.17°C, SE = 1.44; *n* = 47). Although the mean difference between snake body temperatures and ambient was minor (mean = 0.71°C), snake body temperatures commonly were much higher than ambient temperatures (e.g. in 64% of cases, snakes averaged 3.07°C warmer than the ambient recording (range 0.12–10.13°C), suggesting that tree hollows might offer distinctive thermal regimes.

Loss of data-loggers restricted our data set to one copper model on the ground in full sun, one from a cavity in a live tree, and two from cavities in dead trees. Tree-cavity temperatures (especially inside the live tree) were less variable over the diel cycle than were those recorded on the ground in full sunlight, or (more interestingly) from cavities in dead trees (Figure 2). Hence, Pale-headed Snakes may be able to select retreat-sites from among a wide thermal range.

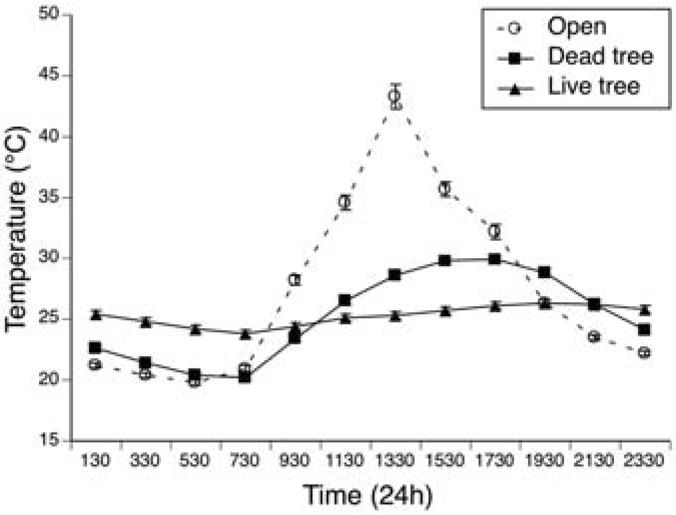

Figure 2. Diel cycles of temperature in habitats used by Pale-headed Snakes. The graph shows two-hourly mean values (plus standard errors) for temperatures monitored inside hollows of live and dead trees, and on open (sun-exposed) ground.

Discussion

Our study is preliminary, based on only a single study site and a single season, and provides data on habitat use and movement patterns on only a few animals. Nonetheless, ours is the first such study ever conducted on this species, and warrants analysis. Some of the behaviours that we observed in our radio-tracked snakes (e.g. arboreality, cryptic sequestration and infrequent movements between shelter-sites) are similar to those revealed by previous studies of the two other members of the genus *Hoplocephalus* (Webb and Shine 1997a,b; Fitzgerald *et al.* 2002a). Nonetheless, some details of the ecology of this species (and probably, their congeneric taxa) may differ considerably among habitat types. For example, Pale-headed Snakes are recorded in the Pilliga Scrub from Narrow-leaved Ironbark/cypress pine habitats on sandy substrate, where tree shelter characteristics and the availability of different prey types (more lizards, especially geckos: M. Fitzgerald, pers. obs.) may substantially affect shelter site selection, foraging locations and the distances moved between trees. Nonetheless, major riverine floodplain habitats may represent core habitat for Pale-headed Snakes.

We radio-tracked snakes only in summer and autumn (December to April), and behaviour may change outside this period. Prolonged overwinter sequestration is common in adult *H. bungaroides* and *H. stephensii* (Webb and Shine 1997a,b; Fitzgerald *et al.* 2002b), although juvenile *H. bungaroides* continue to be active and to feed throughout winter (Webb and Shine 1997a). Records of juvenile and subadult pale-headed snakes beneath decorticating bark during the day (B. Lazell, pers. obs.) suggest that shelter site use may change ontogenetically in Pale-headed Snakes.

Like their congeners, Pale-headed Snakes often remain hidden in tree hollows for long periods. Sequestration during the active season lasted for up to 52 days for *H. stephensii* (Fitzgerald *et al.* 2002a) and up to 48 days for *H. bungaroides* (Webb and Shine 1997a,b). Our data, although limited, suggest that this kind of sequestration behaviour is likely to be consistent within the genus. Why do *Hoplocephalus* spend such long periods inactive within tree-hollows or other retreat-sites? Advantages may include avoidance of predators, conservation of energy, access to arboreal prey species and abiotic (e.g. thermal, hydric) benefits. For example, tree hollows provide stable moist conditions (Sedgely 2001). Our data on thermal regimes within tree hollows accord well with this suggestion. Radio-tracked snakes in live tree cavities exhibited body temperatures from 17.9–33.5°C (averaging 25.8°C) whereas thermal regimes in a cavity within a dead tree were hotter and more variable (see Figure 2), and temperatures of a model (copper) snake on the ground in full sunlight rapidly heated to lethal levels (24% of copper model temperatures >40°C). Thus, hollows in live trees may provide buffered thermal regimes for Pale-headed Snakes, as they do for congeneric species (Webb and Shine 1998b; Fitzgerald *et al.* 2003). Although based on a much more limited data set, our estimate for mean active season body temperature for Pale-headed Snakes (25.8°C) is similar to that reported for *H. bungaroides* (25.6°C; Webb and Shine 1998b) and *H. stephensii* (24.0°C; Fitzgerald *et al.* 2003).

Is the Pale-headed Snake a species of conservation concern, as predicted by Reed and Shine's (2002) analysis? We believe that it is. Because Pale-headed Snakes appear to be obligate tree hollow dwellers, the most obvious threat is removal of trees. In the vicinity of the study site (and presumably elsewhere in the species range, e.g. Queensland Brigalow Belt), large areas of native floodplain woodland have been cleared for agriculture. At survey sites east of Narrabri (Spring Creek, Bobbiwa Creek) where the species was recorded during the early 1990s, riparian vegetation has been reduced to a single row of mature trees along the riverbank, with few recruit trees, and tree regeneration largely suppressed by grazing/browsing (M. Fitzgerald pers. obs.). The decline of hollow-bearing trees and ultimate lack of replacement trees will eliminate populations of Pale-headed Snakes by removal of essential shelter sites. Another threat involves reduced flows in major inland rivers, apparently due to excessive offtake of water for agricultural use (Flannery 1994). Deaths of extensive River Red Gum forests have been reported, with obvious implications for the viability of faunal populations that depend upon this distinctive habitat. Lastly, the species also may be vulnerable to invasive Cane Toads *Bufo* (*Rhinella*) *marinus*. The snakes feed primarily on frogs and may thus be expected to attack toads. All Australian elapids tested to date have proved so sensitive to the toad's toxin that they are unlikely to survive ingesting a medium-sized toad (Phillips *et al*. 2003). Recent modelling suggests that cane toads ultimately may invade much of the area currently occupied by Pale-headed Snakes (Urban *et al.* 2007). We thus suggest that further, more detailed studies on the ecology and conservation status of Pale-headed Snakes deserve high priority.

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